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Disturbance Ecology

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Abstract

Questions

We tested the relationship between total cover, species richness and composition of epiphytic lichens on trunks of *Betula pubescens* and ecosystem retrogression (i.e. prolonged absence of major disturbance). We then investigated how the relationships changed when also accounting for tree-scale factors (aspect, height and bark characteristics) and ecosystem-scale factors (e.g. light transmission, tree species diversity and soil fertility).

Location

Thirty forested islands in northern Sweden differing in fire history, which collectively represent a retrogressive chronosequence spanning ca. 5000 yr.

Results

Total lichen cover responded negatively to long-term absence of major disturbance, but only at exposed positions on the tree trunk, indicating that lichen cover on substrates with more favourable microclimates is less susceptible to environmental change at the ecosystem scale. Further, although there was no overall effect of island size on lichen species richness, we did find a significant interactive effect between island size and height on trunk on species richness. This emerged because species richness decreased with retrogression for lichen communities at breast height, but showed a hump-shaped response to retrogression at the trunk base. Shifts in ecosystem properties with retrogression explained some of the variation in lichen community composition, but most of the variation could be explained by tree-scale factors, notably height on the trunk.

Conclusions

While it has frequently been shown that lichens increase in abundance and richness during the first two or three centuries of succession, our results highlight that over a much longer time scale, encompassing soil aging and declining soil fertility, the lichen flora can be negatively affected. However, these effects are heavily mediated by tree-scale factors. These changes in the lichen community may be of potential importance for ecosystem processes and higher trophic level interactions driven by lichen communities.

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Averett, J. P., et al. (2016). "Non-Native Plant Invasion along Elevation and Canopy Closure Gradients in a Middle Rocky Mountain Ecosystem." *PloS one* 11(1): e0147826.

Mountain environments are currently among the ecosystems least invaded by non-native species; however, mountains are increasingly under threat of non-native plant invasion. The slow pace of exotic plant invasions in mountain ecosystems is likely due to a combination of low anthropogenic disturbances, low propagule supply, and extreme/steep environmental gradients. The importance of any one of these factors is debated and likely ecosystem dependent. We evaluated the importance of various correlates of plant invasions in the Wallowa Mountain Range of northeastern Oregon and explored whether non-native species distributions differed from native species along an elevation gradient. Vascular plant communities were sampled in summer 2012 along three mountain roads. Transects (n = 20) were evenly stratified by elevation (~70 m intervals) along each road. Vascular plant species abundances and environmental parameters were measured. We used indicator species analysis to identify habitat affinities for non-native species. Plots were ordinated in species space, joint plots and non-parametric multiplicative regression were used to relate species and community variation to environmental variables. Non-native species richness decreased continuously with increasing elevation. In contrast, native species richness displayed a unimodal distribution with maximum richness occurring at mid-elevations. Species composition was strongly related to elevation

and canopy openness. Overlays of trait and environmental factors onto non-metric multidimensional ordinations identified the montane-subalpine community transition and over-story canopy closure exceeding 60% as potential barriers to non-native species establishment. Unlike native species, non-native species showed little evidence for high-elevation or closed-canopy specialization. These data suggest that non-native plants currently found in the Wallowa Mountains are dependent on open canopies and disturbance for establishment in low and mid elevations. Current management objectives including restoration to more open canopies in dry Rocky Mountain forests, may increase immigration pressure of non-native plants from lower elevations into the montane and subalpine zones.

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Beaver (*Castor* spp.) conservation requires an understanding of their complex interactions with competing herbivores. Simulation modeling offers a controlled environment to examine long-term dynamics in ecosystems driven by uncontrollable variables. We used a new version of the SAVANNA ecosystem model to investigate beaver (*C. canadensis*) and elk (*Cervus elaphus*) competition for willow (*Salix* spp.). We initialized the model with field data from Rocky Mountain National Park, Colorado, USA, to simulate a 4-ha riparian ecosystem containing beaver, elk, and willow. We found beaver persisted indefinitely when elk density was ≤ 20 elk km⁻². Beaver persistence decreased exponentially as elk density increased from 30 to 60 elk km⁻², which suggests the presence of an ecological threshold. The interaction of beaver and elk herbivory shifted the size distribution of willow plants from tall to short when elk densities were ≥ 30 elk km⁻². The loss of tall willow preceded rapid beaver declines, thus willow condition may predict beaver population trajectory in natural environments. Beaver were able to persist with slightly higher elk densities if beaver alternated their use of foraging sites in a rest-rotation pattern rather than maintained continuous use. Thus, we found asymmetrical competition for willow strongly favored elk over beaver in a simulated montane ecosystem. Finally, we discuss application of the SAVANNA model and mechanisms of competition relative to beaver persistence as metapopulations, ecological resistance and alternative state models, and ecosystem regulation.

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Climatic changes at Coringa-Herald National Nature Reserve (CHNNR) in the last 82 yr include a 0.7- ∞ C rise in mean minimum winter temperatures and increases in drought duration and frequency. Between 1991 and 2002, a plague of the scale insects *Pulvinaria urbicola* (Cockerell), together with attendant ants destroyed *Pisonia grandis* R.Br, rain forest at South-West Coringa Islet. Scale insect damage of *P. grandis* has also been recorded at North-East Herald Cay. This study explored the reasons for vegetation dieback during current climate. Woody species such as *Argusia argentea* (L.) Heine, *Cordia subcordata* Lam., and the grasses *Lepturus repens* (G. Forst.) R.Br. and *Stenotaphrum micranthum* (Desv.) C. E. Hubb. have also declined at CHNNR. *Ximenia americana* L. and *Digitaria ctenantha* (F. Muell.) Hughes were found to be locally extinct. Dieback of forests results in reduction of canopy-breeding seabirds and burrowing shearwaters (*Puffinus pacificus* [Gmelin]). Dieback species were replaced by the shrub *Abutilon albescens* Miq. and/or fleshy herbaceous plants such as *Achyranthes aspera* L., *Boerhavia albiflora* Fosberg, *Ipomoea micrantha* Roem. & Schult, *Portulaca oleracea* L., and *Tribulus cistoides* L. Increasing duration of droughts and increased temperatures, together with damage caused by exotic insect pests, appear to be the key drivers of the current vegetation changes.

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<P.abies has migrated south over this period, has replaced mixed h...>

Black, S. H., et al. (2013). "Do bark beetle outbreaks increase wildfire risks in the central Rocky Mountains? Implications from recent research." *Natural Areas* 33(1): 59-65.

Appropriate response to recent, widespread bark beetle (*Dendroctonus* spp.) outbreaks in the western United States has been the subject of much debate in scientific and policy circles. Among the proposed responses have been landscape-level mechanical treatments to prevent the further spread of outbreaks and to reduce the fire risk that is believed to be associated with insect-killed trees. We review the literature on the efficacy of silvicultural practices to control outbreaks and on fire risk following bark beetle outbreaks in several forest types. While research is ongoing and important questions remain unresolved, to date most available evidence indicates that bark beetle outbreaks do not substantially increase the risk of active crown fire in lodgepole pine (*Pinus contorta*) and spruce (*Picea engelmannii*)-fir (*Abies* spp.) forests under most conditions. Instead, active crown fires in these forest types are primarily contingent on dry conditions rather than variations in stand structure, such as those brought about by outbreaks. Preemptive thinning may reduce susceptibility to small outbreaks but is unlikely to reduce susceptibility to large, landscape-scale epidemics. Once beetle populations reach widespread epidemic levels, silvicultural strategies aimed at stopping them are not likely to reduce forest susceptibility to outbreaks. Furthermore, such silvicultural treatments could have substantial, unintended short- and long-term ecological costs associated with road access and an overall degradation of natural areas.

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Bone, C., et al. (2016). "Employing resilience in the United States Forest Service." *Land Use Policy* 52: 430-438.

The concept of resilience has permeated the discourse of many land use and environmental agencies in an attempt to articulate how to develop and implement policies concerned with the social and ecological dimensions of natural disturbances. Several distinct definitions of resilience exist, each with its own concepts, focus and contexts related to land use policy and management. This often makes understanding the inherent objectives of policies and related principles challenging. The United States Forest Service (USFS) is one example where ambiguity and uncertainty surrounding the use of resilience permeates the content of documents in various areas of the agency. The objective of this paper is to investigate how the USFS employs the term resilience as a means to communicate strategies for managing forest lands. We perform a content analysis of 121 USFS documents including budgetary justification reports, research findings (i.e., journal articles, book chapters and technical reports), public releases, and newsletters to analyze both the rise and specific use of the term resilience in the USFS. Our analysis, which is guided by definitions of resilience in the social-ecological systems literature, reveals that the ambiguity surrounding the use of resilience in the academic literature is reflected in the content of USFS documents. However, we also find that often criticized versions of resilience (namely engineering resilience) are minimally employed by the USFS, and instead the agency focuses on the notion of ecological resilience in which natural disturbances are seen as an important component of the landscape. In some cases, the USFS

employs notions of social-ecological resilience, however, the extent to which specific components of social-ecological resilience are integrated into management strategies appears minimal. The findings from this study suggest that clarity regarding the type and function of resilience needs to improve in USFS documents, and that the agency should evaluate the existing question in the SES literature of resilience of what to what?

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Learning is a fundamental driver and product of adaptive management. We measured organizational learning attributes in a survey of US Forest Service employees in 2008 to assess the agency learning environment by organizational hierarchy and work unit in the agency and to benchmark the US Forest Service against other external organizations. We found that positive organizational learning attributes are unevenly distributed throughout the agency's work units and hierarchy. US Forest Service managers experience a stronger learning environment than staff, and work units in the National Forest System have significantly weaker learning environments than research stations and state and private forestry. Furthermore, US Forest Service learning attributes fall below the median compared with external benchmark scores. We offer some general suggestions for improving the learning environment in the agency but we are

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We synthesize insights from current understanding of drought impacts at stand-to-biogeographic scales, including management options, and we identify challenges to be addressed with new research. Large stand-level shifts underway in western forests already are showing the importance of interactions involving drought, insects, and fire. Diebacks, changes in composition and structure, and shifting range limits are widely observed. In the eastern US, the effects of increasing drought are becoming better understood at the level of individual trees, but this knowledge cannot yet be confidently translated to predictions of changing structure and diversity of forest stands. While eastern forests have not experienced the types of changes seen in western forests in recent decades, they too are vulnerable to drought and could experience significant changes with increased severity, frequency, or duration in drought. Throughout the continental United States, the combination of projected large climate-induced shifts in suitable habitat from modeling studies and limited potential for the rapid migration of tree populations suggests that changing tree and forest biogeography could substantially lag habitat shifts already underway. Forest management practices can partially ameliorate drought impacts through reductions in stand density, selection of drought-tolerant species and genotypes, artificial regeneration, and the development of multistructured stands. However,

silvicultural treatments also could exacerbate drought impacts unless implemented with careful attention to site and stand characteristics. Gaps in our understanding should motivate new research on the effects of interactions involving climate and other species at the stand scale and how interactions and multiple responses are represented in models. This assessment indicates that, without a stronger empirical basis for drought impacts at the stand scale, more complex models may provide limited guidance.

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There is widespread concern that fire exclusion has led to an unprecedented threat of uncharacteristically severe fires in ponderosa pine (*Pinus ponderosa* Dougl. ex. Laws) and mixed-conifer forests of western North America. These extensive montane forests are considered to be adapted to a low/moderate-severity fire regime that maintained stands of relatively old trees. However, there is increasing recognition from landscape-scale assessments that, prior to any significant effects of fire exclusion, fires and forest structure were more variable in these forests. Biota in these forests are also dependent on the resources made available by higher-severity fire. A better understanding of historical fire regimes in the ponderosa pine and mixed-conifer forests of western North America is therefore needed to define reference conditions and help maintain characteristic ecological diversity of these systems. We compiled landscape-scale evidence of historical fire severity patterns in the ponderosa pine and mixed-conifer forests from published literature sources and stand ages available from the Forest Inventory and Analysis program in the USA. The consensus from this evidence is that the traditional reference conditions of low-severity fire

regimes are inaccurate for most forests of western North America. Instead, most forests appear to have been characterized by mixed-severity fire that included ecologically significant amounts of weather-driven, high-severity fire. Diverse forests in different stages of succession, with a high proportion in relatively young stages, occurred prior to fire exclusion. Over the past century, successional diversity created by fire decreased. Our findings suggest that ecological management goals that incorporate successional diversity created by fire may support characteristic biodiversity, whereas current attempts to 'restore' forests to open, low-severity fire conditions may not align with historical reference conditions in most ponderosa pine and mixed-conifer forests of western North America.

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Increasingly, forest management goals include building or maintaining resistance and/or resilience to disturbances in the face of climate change. Although a multitude of descriptive definitions for resistance and resilience exist, to evaluate whether specific management activities (silviculture) are effective, prescriptive characterizations are necessary. We introduce a conceptual framework that explicitly differentiates resistance and resilience, denotes appropriate scales, and establishes the context for evaluation, 'structure and composition. Generally, resistance is characterized as the influence of structure and composition on disturbance, whereas resilience is characterized as the influence of disturbance on subsequent structure and composition. Silvicultural utility of the framework is demonstrated by describing disturbance-specific, time-bound structural and compositional objectives for building resistance and resilience to two fundamentally different disturbances: wildfires and spruce beetle outbreaks. The conceptual framework revealed the crucial insight that attempts to build stand or landscape resistance to spruce beetle outbreaks will ultimately be unsuccessful. This frees the silviculturist to focus on realistic goals associated with building resilience to likely inevitable outbreaks. Ultimately, because structure and composition, at appropriate scales, are presented as the standards for evaluation and manipulation, the framework is broadly applicable to many kinds of disturbance in various forest types.

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Citizen science, the involvement of volunteers in research, has increased the scale of ecological field studies with continent-wide, centralized monitoring efforts and, more rarely, tapping of volunteers to conduct large, coordinated, field experiments. The unique benefit for the field of ecology lies in understanding processes occurring at broad geographic scales and on private lands, which are impossible to sample extensively with traditional field research

models. Citizen science produces large, longitudinal data sets, whose potential for error and bias is poorly understood. Because it does not usually aim to uncover mechanisms underlying ecological patterns, citizen science is best viewed as complementary to more localized, hypothesis-driven research. In the process of addressing the impacts of current, global "experiments" altering habitat and climate, large-scale citizen science has led to new, quantitative approaches to emerging questions about the distribution and abundance of organisms across space and time.

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Decisions always involve both facts and values, whereas most science communication focuses only on facts. If science communication is intended to inform decisions, it must be competent with regard to both facts and values. Public participation inevitably involves both facts and values. Research on public participation suggests that linking scientific analysis to public deliberation in an iterative process can help decision making deal effectively with both facts and values. Thus, linked analysis and deliberation can be an effective tool for science communication. However, challenges remain in conducting such process at the national and global scales, in enhancing trust, and in reconciling diverse values.

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Aim

In managed forest landscapes, the tolerance of species to contemporary alteration of forest cover is often assumed to reflect their resilience to natural disturbances. We tested this central tenet of ecosystem-based management by comparing the structure of forest bird assemblages among four regions with contrasting historical natural disturbance regimes.

Location

Canada's boreal and northern hardwood forests.

Methods

Using point count data from four study regions across Canada, we first determined the relative sensitivity of individual bird species to the contemporary reduction of old forest cover at stand and "landscape-context" (1-km radius) scales with log-linear models. The richness of species most sensitive to loss of old forest (hereafter "sensitive species") was then modelled as a function of landscape-scale changes in old forest cover. Differences in the rate of decline in the richness of sensitive species with contemporary cover of old forest were compared among regions using ANCOVA. We then compared broken-stick regression models with linear models to detect thresholds, if present, in this relationship in each region.

Results

Bird assemblages from regions with relatively infrequent natural disturbances hosted more species sensitive to contemporary reduction in old forest cover. Those species were also more abundant than in regions with

frequent natural disturbances, and the rate of decline in their richness with the loss of old forest was steeper in regions with infrequent natural disturbances than in those where they were frequent. However, we did not detect thresholds in this rate of decline in any study region.

Main conclusions

Our findings are consistent with the contention that historical natural disturbance regimes shape the response of biota to contemporary landscape alterations through evolutionary adaptation. We argue that forest management conducted within the natural range of variability in stand and landscape structure specific to a region is likely to be ecologically sustainable.

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independent from surface observations. It was found that the proportion of winter (January,ÀiMarch) precipitation falling as snow has decreased by 9% during the last half century, a combined result from a significant increase in rainfall and a minor decrease in snowfall. Meanwhile, observed snow depth across Utah has decreased and is accompanied by consistent decreases in snow cover and surface albedo. Weather systems with the potential to produce precipitation in Utah have decreased in number with those producing snowfall decreasing at a considerably greater rate. Further circulation analysis showed that an anomalous anticyclone has developed over western North America, which acts to reduce the frequency of cyclone waves impacting Utah. Combined with the increased precipitation, this feature suggests that the average precipitation per event has intensified with more of it falling as rain than as snow. Trends in the hydroclimate such as these have implications for present and future regional water policy in the state of Utah.

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Ecological memory is central to how ecosystems respond to disturbance and is maintained by two types of legacies, information and material. Species life-history traits represent an adaptive response to disturbance and are an information legacy; in contrast, the abiotic and biotic structures (such as seeds or nutrients) produced by single disturbance events are material legacies. Disturbance characteristics that support or maintain these legacies enhance ecological resilience and maintain a "safe operating space" for ecosystem recovery. However, legacies can be lost or diminished as disturbance regimes and environmental conditions change, generating a "resilience debt" that manifests only after the system is disturbed. Strong effects of ecological memory on post-disturbance dynamics imply that contingencies (effects that cannot be predicted with certainty) of individual disturbances, interactions among disturbances, and climate variability combine to affect ecosystem resilience. We illustrate these concepts and introduce a novel ecosystem resilience framework with examples of forest disturbances, primarily from North America. Identifying legacies that support resilience in a particular ecosystem can help scientists and resource managers anticipate when disturbances may trigger abrupt shifts in forest ecosystems, and when forests are likely to be resilient.

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The Colorado National Monument (COLM), on the northeastern edge of the Uncompahgre Plateau, supports a persistent Piñon (Pinus edulis Engelm.) and juniper (Juniperus osteosperma (Torr.) Little) woodland, which has not been disturbed by large stand-replacing fires since modern fire records began. We examined the fire history of large (> 100 ha) stand-replacing fires, documented tree population structures, and characterized tree density, quadratic mean diameter (QMD), relative composition, and cumulative mortality using 431 0.1-haplots distributed over 1600 ha of the Monument. We found no evidence of large stand-replacing fires (charred wood or truncated stand structures) in the study area. Stand ages inferred from size structures suggest that large stand-replacing fires have been absent for possibly a millennia. Tree population structures show a more stable stand structure for juniper; Piñon pine population structures show a more recent and sustained regeneration pulse. Cumulative mortality of Piñon pines was 18%, peaking at 47% in trees 20 to 24.5 cm diameter. Spatial patterns of juniper density, QMD, and mortality were more homogeneous than those of Piñon pine. Results suggest temporal dynamics and spatial patterns of the COLM woodland are more influenced by drought and small fires (< 10 ha) than large fires (> 100 ha). This study provides important baseline data for changes that may be brought about by climate change in coming decades. It also stresses the importance of controlling cheatgrass (Bromus tectorum) and other invasive species to increase resistance of these persistent Piñon-juniper woodlands to future fires.

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Wildlife habituation near urban centers can disrupt natural ecological processes, destroy habitat, and threaten public safety. Consequently, management of habituated animals is typically invasive and often includes translocation of these animals to remote areas and sometimes even their destruction. Techniques to prevent or reverse habituation and other forms of in situ management are necessary to balance ecological and social requirements, but they have received very little experimental attention to date. This study compared the efficacy of two aversive conditioning treatments that used either humans or dogs to create sequences resembling chases by predators, which, along with a control category, were repeatedly and individually applied to 24 moderately habituated, radio-collared elk in Banff National Park during the winter of 2001-2002. Three response variables were measured before and after treatment. Relative to untreated animals, the distance at which elk fled from approaching humans, i.e., the flight response distance, increased following both human and dog treatments, but there was no difference between the two treatments. The proportion of time spent in vigilance postures decreased for all treatment groups, without differences among groups, suggesting that this behavior responded mainly to seasonal effects. The average distance between elk locations and the town boundary, measured once daily by telemetry, significantly increased for human-conditioned elk. One of the co-variables we measured, wolf activity, exerted

counteracting effects on conditioning effects; flight response distances and proximity to the town site were both lower when wolf activity was high. This research demonstrates that it is possible to temporarily modify aspects of the behavior of moderately habituated elk using aversive conditioning, suggests a method for reducing habituation in the first place, and provides a solution for Banff and other jurisdictions to manage hyperabundant and habituated urban wildlife.

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The frequency, magnitude, and size of forest disturbances are increasing globally. Much recent research has focused on how the occurrence of one disturbance may affect susceptibility to subsequent disturbances. While much has been learned about such linked disturbances, the strength of the interactions is likely to be contingent on the severity of disturbances as well as climatic conditions, both of which can affect disturbance intensity and tree resistance to disturbances. Subalpine forests in western Colorado were

affected by extensive and severe wildfires in the late 19th century and an extensive and severe outbreak of spruce beetle (*Dendroctonus rufipennis*) in the 1940s. Previous research found that most, but not all, of the stands that burned and established following the late 19th century fires were not susceptible to the 1940s outbreak as beetles preferentially attack larger trees and stands in advanced stages of development. However, previous research also left open the possibility that some stands that burned and established following the 19th century fires may have been attacked during the 1940s outbreak. Understanding how strongly stand structure, as shaped by disturbances of varying severity, affected susceptibility to past outbreaks is important to provide a baseline for assessing the degree to which recent climate change may be relaxing the preferences of beetles for larger trees and for stands in latter stages of structural development and thereby changing the nature of linked disturbances. Here, dendroecological methods were used to study disturbance history and tree age of stands in the White River National Forest in Western Colorado that were identified in historical documents or remotely-sensed images as having burned in the 19th century and having been attacked by spruce beetle in the 1940s. Dendroecological reconstructions indicate that in young post-fire stands only old remnant trees that survived the otherwise stand-replacing fires were killed in the 1940s outbreak. No young post-fire trees (< ca. 128 years) were susceptible to the 1940s outbreak, implying that under the relatively cool and wet conditions of the mid-20th century, susceptibility to and spatial patterns of spruce beetle outbreak were most likely controlled by variations in severity of prior disturbance by fire. This study provides a baseline for comparing linked disturbances under the relatively warmer and drier conditions of recent (e.g. post-1990) outbreaks in order to assess how climate mitigates the degree to which pre-disturbance history and structure affect susceptibility to disturbances.

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By analyzing interview and survey data from 1,640 US Department of Agriculture (USDA) Forest Service employees across three management levels, we assessed their perceptions, actions, concerns, and needs regarding incorporating climate change into managing the National Forests. We found that regional- and forest-level employees tend to think climate change presents new challenges and requires new approaches to address it, whereas on-the-ground managers tend to view it as a buzzword and want more flexibility to continue doing what they do. We found that forest managers have been engaged in conversation and thinking about climate change but few on-the-ground actions. Our study suggests a need for incorporating local staff knowledge into agency decisionmaking, establishing common ground within the agency by promoting climate change initiatives in the context of enhancing forest resilience, providing more scale-relevant data, research, training, and guidance, and developing strategies that enable forest managers to address management challenges that interact with climate change.

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Hunting by humans can be a potent driver of selection for morphological and life history traits in wildlife populations across continents and taxa. Few studies, however, have documented selection on behavioural responses that increase individual survival under human hunting pressure. Using habitat with dense concealing cover is a common strategy for risk avoidance, with a higher chance of survival being the payoff. At the same time, risk avoidance can be costly in terms of missed foraging opportunities. We investigated individual fine-scale use of habitat by 40 GPS-marked European red deer, *Cervus elaphus*, and linked this to their survival through the hunting season. Whereas all males used similar habitat in the days before the hunting season, the onset of hunting induced an immediate switch to habitat with more concealing cover in surviving males, but not in males that were later shot. This habitat switch also involved a trade-off with foraging opportunities on bilberry, *Vaccinium myrtillus*, a key forage plant in autumn. Moreover, deer that use safer forest habitat might survive better because they make safer choices in general. The lack of a corresponding pattern in females might be because females were already largely using cover when hunting started, as predicted by sexual segregation theory and the risk of losing offspring. The behavioural response of males to the onset of hunting appears to be adaptive, given that it is linked to increased survival, an important fitness component. We suggest that predictable harvesting regimes with high harvest rates could create a strong selective pressure for deer to respond dynamically to the temporal change in hunting risk. Management should consider the potential for both ecological and evolutionary consequences of harvesting regimes on behaviour.

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ABSTRACT Off-road recreation on public lands in North America has increased dramatically in recent years. Wild ungulates are sensitive to human activities, but the effect of off-road recreation, both motorized and nonmotorized, is poorly understood. We measured responses of elk (*Cervus elaphus*) to recreational disturbance in northeast Oregon, USA, from April to October, 2003 and 2004. We subjected elk to 4 types of recreational disturbance: all-terrain vehicle (ATV) riding, mountain biking, hiking, and horseback riding. Motion sensors inside radiocollars worn by 13 female elk recorded resting, feeding, and travel activities at 5-minute intervals throughout disturbance and control periods. Elk fed and rested during control periods, with little time spent traveling. Travel time increased in response to all 4 disturbances and was highest in mornings. Elk travel time was highest during ATV exposure, followed by exposure to mountain biking, hiking, and horseback riding. Feeding time decreased during ATV exposure and resting decreased when we subjected elk to mountain biking and hiking disturbance in 2003. Our results demonstrated that activities of elk can be substantially affected by off-road recreation. Mitigating these effects may be appropriate where elk are a management priority. Balancing management of species like elk with off-road recreation will become increasingly important as off-road recreational uses continue to increase on public lands in North America.

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Hurlbert divides experimental ecologists into "those who do not see any need for dispersion (of replicated treatments and controls), and those who do recognize its importance and take whatever measures are necessary to achieve a good dose of it." Experimental ecologists could also be divided into those who do not see any problems with sacrificing spatial and temporal scales in order to obtain replication, and those who understand that appropriate scale must always have priority over replication. If an experiment is conducted in a spatial or temporal scale, where the predictions of contesting hypotheses are convergent or ambiguous, no amount of technical impeccability can make the work instructive. Conversely, replication can always be obtained afterwards, by conducting more experiments with basically similar design in different areas and by using meta-analysis. This approach even reduces the sampling bias obtained if resources are allocated to a small number of well-replicated experiments. For a strict advocate of the hypothetico-deductive method, replication is unnecessary even as a matter of principle, unless the predicted response is so weak that random background noise is a plausible excuse for a discrepancy between predictions and results. By definition, a prediction is an "all-statement," referring to all systems within a well-defined category. What applies to all must apply to any. Hence, choosing two systems and assigning them randomly to a treatment and a control is normally an adequate design for a deductive experiment. The strength of such experiments depends on the firmness of the predictions and their a priori probability of corroboration. Replication is but one of many ways of reducing this probability. Whether the experiment is replicated or not, inferential statistics should always be used, to enable the reader to judge how well the apparent patterns in samples reflect real patterns in statistical populations. The concept "pseudoreplication" amounts to entirely unwarranted stigmatization of a reasonable way to test predictions referring to large-scale systems.

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We explored multiple linkages among grey wolves (*Canis lupus*), elk (*Cervus elaphus*), berry-producing shrubs and grizzly bears (*Ursus arctos*) in Yellowstone National Park.

We hypothesized competition between elk and grizzly bears whereby, in the absence of wolves, increases in elk numbers would increase browsing on berry-producing shrubs and decrease fruit availability to grizzly bears. After wolves were reintroduced and with a reduced elk population, we hypothesized there would be an increase in the establishment of berry-producing shrubs, such as serviceberry (*Amelanchier alnifolia*), which is a major berry-producing plant. We also hypothesized that the percentage fruit in the grizzly bear diet would be greater after than before wolf reintroduction.

We compared the frequency of fruit in grizzly bear scats to elk densities prior to wolf reintroduction during a time of increasing elk densities (1968,–1987). For a period after wolf reintroduction, we calculated the percentage fruit in grizzly bear scat by month based on scats collected in 2007,–2009 (n = 778 scats) and compared these results to scat data collected before wolf reintroduction. Additionally, we developed an age structure for serviceberry showing the origination year of stems in a northern range study area.

We found that over a 19-year period, the percentage frequency of fruit in the grizzly diet (6231 scats) was inversely correlated ($P < 0.001$) with elk population size. The average percentage fruit in grizzly bear scats

was higher after wolf reintroduction in July (0→3% vs. 5→9%) and August (7→8% vs. 14→6%) than before. All measured serviceberry stems accessible to ungulates originated since wolf reintroduction, while protected serviceberry growing in a nearby ungulate exclosure originated both before and after wolf reintroduction. Moreover, in recent years, browsing of serviceberry outside of the exclosure decreased while their heights increased.

Overall, these results are consistent with a trophic cascade involving increased predation by wolves and other large carnivores on elk, a reduced and redistributed elk population, decreased herbivory and increased production of plant-based foods that may aid threatened grizzly bears.

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Pseudoreplication is one of the most influential methodological issues in ecological and animal behavior research today. At its inception, the idea of pseudoreplication highlighted important concerns about the design and analysis of experiments in ecology. The doctrine purported to provide a unified view of experimental design and analysis, wherein precise criteria could be used to assess manuscripts and research proposals for acceptance or rejection. Few methodological doctrines have had as much impact as pseudoreplication, yet there has been very little critical analysis of it. In this paper, the authors extend the growing criticism of the concept of pseudoreplication. The authors argue that the core ideas behind pseudoreplication are based on a misunderstanding of statistical independence, the nature of control groups in science, and contexts of statistical inference. The authors also highlight how other areas of research have found and responded to similar issues in the design and analysis of experiments through the use of more advanced statistical methods. Ultimately, there are no universal criteria for accepting or rejecting experimental research; all research must be judged on its own merits.

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While the use of timber harvests is generally accepted as an effective approach to controlling bark beetles during outbreaks, in reality there has been a dearth of monitoring to assess outcomes, and failures are often not reported. Additionally, few studies have focused on how these treatments affect forest structure and function over the long term, or our forests' ability to adapt to climate change. Despite this, there is a widespread belief in the policy arena that timber harvesting is an effective and necessary tool to address beetle infestations. That belief has led to numerous proposals for, and enactment of, significant changes in federal environmental laws to encourage more timber harvests for beetle control. In this review, we use mountain pine beetle as an exemplar to critically evaluate the state of science behind the use of timber harvest treatments for bark beetle suppression during outbreaks. It is our hope that this review will stimulate research to fill important gaps and to help guide the development of policy and management firmly based in science, and thus, more likely to aid in forest conservation, reduce financial waste, and bolster public trust in public agency decision-making and practice.

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Small, B. A., et al. (2016). "Livestock grazing limits beaver restoration in northern New Mexico." *Restoration Ecology*.

The North American beaver (*Castor canadensis*) builds dams that pond water on streams, which provide crucial ecological services to aquatic and riparian ecosystems and enhance biodiversity. Consequently, there is increasing interest in restoring beavers to locations where they historically occurred, particularly in the arid western United States. However, despite often intensive efforts to reintroduce beavers into areas where they were severely reduced in numbers or eliminated due to overharvesting in the eighteenth and nineteenth centuries, beavers remain sparse or missing from many stream reaches. Reasons for this failure have not been well studied. Our goal was to evaluate certain biotic factors that may limit the occurrence of dam-building beavers in northern New Mexico, including competitors and availability of summer and winter forage. We compared these factors at primary active dams and at control sites located in stream reaches that were physically suitable for dam-building beavers but where none occurred. Beaver dams mostly occurred at sites that were not grazed or where there was some alternative grazing management, but were mostly absent at sites within Forest Service cattle allotments. Results indicated that cattle grazing influenced the relation between vegetation variables and beaver presence. The availability of willows (*Salix* spp.) was the most important plant variable for the presence of beaver dams. We conclude that grazing by cattle as currently practiced on Forest Service allotments disrupts the beaver-willow mutualism, rendering stream reaches unsuitable for dam-building beavers. We recommend that beaver restoration will require changes to current livestock management practices.

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Smith, J. M., et al. (2015). "Permanent forest plots show accelerating tree mortality in subalpine forests of the Colorado Front Range from 1982 to 2013." *Forest Ecology and Management* 341: 8-17.

Broad-scale studies have documented widespread increases in tree mortality coincident with warming in the western U.S.A., but variability in patterns and agents of mortality is poorly documented based on multi-decadal observations of permanently marked trees, particularly in Rocky Mountain subalpine forests. The current study examines temporal variability in tree mortality based on monitoring >5000 permanently marked trees across a range of topographic positions and stand ages from c. 120 to >550 years over a 31-year period in subalpine forests in the Colorado Front Range. This study documents accelerating rates of annual tree mortality for subalpine fir, Engelmann spruce, lodgepole pine, and limber pine from 1982 through 2013. Over the period from 1982 to 2013, annual mortality rates for all tree species combined increased from 0.36% to 1.03% in old stands (265 to >550 years since stand-initiating fires) and from 0.30% to 0.72% in young stands (120 years since fire). Tree populations at sites of topographically moister locations and where competition was less due to presence of canopy openings, experienced initially lower rates of tree mortality but all populations experienced higher mortality rates after c. 2008. In comparison with the 1953-1994 period, the frequency of extreme high temperatures in early summer increased after the mid-1970s and more markedly after 2000. Over time, the contribution of early summer (July) conditions to annual drought has increased. This pattern of climatic variability has been coincident with and conducive to a two and a half fold increase in the average annualized tree mortality rates for the total tracked tree population from the relatively cool and wet 1982-1994 period to the warmer and drier 2008-2013 period. Tree mortality attributable to bark beetles over the 1982-2013 period was minor, except for western balsam bark beetle (*Dryocoetes confusus*) which since 2008 has accounted for about 12% of the subalpine fir deaths. Overall, our findings indicate that even in the absence of lethal bark beetle outbreaks conifer mortality, apparently associated with moisture stress, has recently increased in subalpine forests in the Colorado Front Range.

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Abstract Fires are integral to the healthy functioning of most ecosystems and are often poorly understood in policy and management, however, the relationship between floristic composition and habitat structure is intrinsically linked, particularly after fire. The aim of this study was to test whether the variability of habitat structure or floristic composition and abundance in forests at a regional scale can be explained in terms of fire frequency using historical data and experimental prescribed burns. We tested this hypothesis in open eucalypt forests of Fraser Island off the east coast of Australia. Fraser Island dunes show progressive stages in plant succession as access to nutrients decreases across the Island. We found that fire frequency was not a good predictor of floristic composition or abundance across dune systems; rather, its effects were dune specific. In contrast, habitat structure was strongly influenced by fire frequency, independent of dune system. A dense understorey occurred in frequently burnt areas, whereas infrequently burnt areas had a more even distribution of plant heights. Plant communities returned to pre-burn levels of composition and abundances within 6 months of a fire and frequently burnt areas were dominated by early successional species of plant. These ecosystems were characterized by low diversity and frequently burnt areas on the east coast were dominated by *Pteridium*. Greater midstorey canopy cover in low frequency areas reduces light penetration and allows other species to compete more effectively with *Pteridium*. Our results strongly indicate that frequent fires on the Island have resulted in a decrease in relative diversity through dominance of several species. Prescribed fire represents a powerful management tool to shape habitat structure and complexity of Fraser Island forests.

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The effect of climatically-driven plant phenology on mammalian reproduction is one key to predicting species-specific demographic responses to climate change. Large ungulates face their greatest energetic demands from the later stages of pregnancy through weaning, and so in seasonal environments parturition dates should match periods of high primary productivity. Interannual variation in weather influences the quality and timing of forage availability, which can influence neonatal survival. Here, we evaluated macro-scale patterns in reproductive performance of a widely distributed ungulate (mule deer, *Odocoileus*

hemionus) across contrasting climatological regimes using satellite-derived indices of primary productivity and plant phenology over eight degrees of latitude (890 km) in the American Southwest. The dataset comprised > 180,000 animal observations taken from 54 populations over eight years (2004-2011). Regionally, both the start and peak of growing season („Start“ and „Peak“, respectively) are negatively and significantly correlated with latitude, an unusual pattern stemming from a change in the dominance of spring snowmelt in the north to the influence of the North American Monsoon in the south. Corresponding to the timing and variation in both the Start and Peak, mule deer reproduction was latest, lowest, and most variable at lower latitudes where plant phenology is timed to the onset of monsoonal moisture. Parturition dates closely tracked the growing season across space, lagging behind the Start and preceding the Peak by 27 and 23 days, respectively. Mean juvenile production increased, and variation decreased, with increasing latitude. Temporally, juvenile production was best predicted by primary productivity during summer, which encompassed late pregnancy, parturition, and early lactation. Our findings offer a parsimonious explanation of two key reproductive parameters in ungulate demography, timing of parturition and mean annual production, across latitude and changing climatological regimes. Practically, this demonstrates the potential for broad-scale modeling of couplings between climate, plant phenology, and animal populations using space-borne observations.

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Veblen, K. E., et al. (2015). "Contrasting Effects of Different Mammalian Herbivores on Sagebrush Plant Communities." *PLoS One* 10(2): e0118016.

Herbivory by both grazing and browsing ungulates shapes the structure and functioning of terrestrial ecosystems worldwide, and both types of herbivory have been implicated in major ecosystem state changes. Despite the ecological consequences of differences in diets and feeding habits among herbivores, studies that experimentally distinguish effects of grazing from spatially co-occurring, but temporally segregated browsing are extremely rare. Here we use a set of long-term exclosures in northern Utah, USA, to determine how domestic grazers vs. wild ungulate herbivores (including browsers and mixed feeders) affect sagebrush-dominated plant communities that historically covered ~62 million ha in North America. We sampled plant community properties and found that after 22 years grazing and browsing elicited perceptible changes in overall plant community composition and distinct responses by individual plant species. In the woody layer of the plant community, release from winter and spring wild ungulate herbivory increased densities of larger Wyoming big sagebrush (*Artemisia tridentata*, ssp. *wyomingensis*) at the expense of small sagebrush, while disturbance associated with either cattle or wild ungulate activity alone was sufficient to increase bare ground and reduce cover of biological soil crusts. The perennial bunchgrass, bottlebrush squirreltail (*Elymus elymoides*), responded positively to release from summer cattle grazing, and in turn appeared to competitively suppress another more grazing tolerant perennial grass, Sandberg's blue grass (*Poa secunda*). Grazing by domestic cattle also was associated with increased non-native species biomass.

Together, these results illustrate that ungulate herbivory has not caused sagebrush plant communities to undergo dramatic state shifts; however clear, herbivore-driven shifts are evident. In a dry, perennial-dominated system where plant community changes can occur very slowly, our results provide insights into potential long-term trajectories of these plant communities under different large herbivore regimes. Our results can be used to guide long-term management strategies for sagebrush systems and improve habitat for endemic wildlife species such as sage-grouse (*Centrocercus* spp.).

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Context: Many ungulate species exhibit strong site fidelity to previously established areas, particularly females. However, development of the landscape may cause animals to shift their distribution to more secure areas.

Aims: To determine range use dynamics (i.e. size and overlap of core areas and home ranges) of female elk (*Cervus elaphus*) relative to land development features (e.g. roads, well pads, buildings, developments, towns, etc.) after controlling for environmental features (i.e. forest cover).

Methods: During the four-year study, we fitted elk ($n = 165$) with GPS collars annually and programmed collars to attempt one location fix every 3 h (eight locations per day) for one year. Females ($n = 18$) were subsequently recaptured and refitted with GPS collars to provide range use dynamics of individual elk over two to three years. We calculated sizes of core areas and home ranges using adaptive kernel estimators, overlap between annual ranges, and establishment of ranges relative to land development.

Key results: Overlap of annual core areas (48.6%) and home ranges (67.9%) was high despite annual increases in land development. Sizes of core areas and home ranges and annual overlap (i.e. site fidelity) were negatively influenced by land development after controlling for forest cover.

Conclusions: These data reveal that female elk show high levels of site fidelity even in the presence of increasing annual land development. Females did not appear to abandon previously established areas, but used ranges in a manner that minimised interaction with development within these areas based on reductions in range use size and fidelity as land development increased.

Implications: To help mitigate impacts on elk, land development should be minimised and large areas of forest protected so elk can avoid areas associated with human activity.

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The plant biomass of a *Eucalyptus signata*-dominated forest 15 m tall growing on infertile sands off the Queensland coast is characterized in detail. The forest has a biomass of 180 t/ha, 90% of which is found in the nine species achieving > 2.5 m height. Of the total biomass, 42.5 % is below ground. Pteridium

esculentum occupies 41 % of the understorey biomass, with 50 shrub and herb species partitioning the remainder. Dimension analysis of 10-11 individuals of each of three tree species- *Eucalyptus signata*, *E. umbra* subsp. *umbra* and *Banksia aemula*-has served to characterize the above- and below-ground growth forms of each species, and provide regressions of the mass of tree components on easily measured plant parts. The size distribution of tree and shrub stems on the site suggests that the major species have evolved quite different reproductive strategies for maintaining a steady-state population in the face of recurrent fires.

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The relative importance of people and climate in shaping prehistoric fire regimes is debated around the world, and this discussion has helped inform our understanding of past and present ecosystem dynamics. Evidence for extensive anthropogenic burning of temperate closed-canopy forests prior to European settlement is geographically variable, and the factors responsible for this variability are not well resolved. We set out to explain the differences in the influence of prehistoric human-set fires in seasonally dry forest types in the Pacific Northwest, New Zealand, and northern Patagonia by comparing the fire traits of dominant taxa, postfire vegetation recovery, long-term climate trends, and human activities that may have motivated burning. Our analysis suggests that ecological and climatic factors explain much of the differences in how these mesic, dry forests responded to prehistoric anthropogenic burning. Understanding past human-environment interactions at regional scales is an important step for assessing the impact of biomass burning at all scales.

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- Abstract
- Several studies have documented that regional climate warming and the resulting increase in drought stress have triggered increased tree mortality in semiarid forests with unavoidable impacts on regional and global carbon sequestration. Although climate warming is projected to continue into the future, studies examining long-term resilience of semiarid forests against climate change are limited. In this study, long-term forest resilience was defined as the capacity of forest recruitment to compensate for losses from mortality. We observed an obvious change in long-term forest resilience along a local aridity gradient by reconstructing tree growth trend and disturbance history and investigating postdisturbance regeneration in semiarid forests in southern Siberia. In our study, with increased severity of local aridity, forests became vulnerable to drought stress, and regeneration first accelerated and then ceased. Radial growth of trees during 1900-2012 was also relatively stable on the moderately arid site. Furthermore, we found that smaller forest patches always have relatively weaker resilience under the same climatic conditions. Our results imply a relatively higher resilience in arid timberline forest patches than in continuous forests; however, further climate warming and increased drought could possibly cause the disappearance of small forest patches around the arid tree line. This study sheds light on climate change adaptation and provides insight into managing vulnerable semiarid forests.
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